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ON THE MODIFICATION OF CHARACTERS BY CROSSING¹

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IN the early years of Mendelian discovery there was much discussion concerning gametic purity in hybrids, and the question whether unit characters are modified on crossing was keenly debated. Convinced by the numerous instances in which Mendelian characters appear to be unmodified by crossing, many writers came to the conclusion that characters universally segregate without being modified or "contaminated" by association with other characters in the hybrid. That such a conclusion is far too sweeping is, however, indicated by many later results, and there is now a disposition to admit that changes in a character or the breaking up of a character may be effected through crossing. But some writers continue to look upon a unit character as an entity, which is unmodifiable and indestructible by hybridization.

Notwithstanding the admitted belief of Bateson and others that characters may be modified by crossing, I know of no extensive body of evidence that such modifications take place except the work of Castle and Phillips (1914) whose conclusions have not been fully accepted and are chiefly concerned with modification by selection. It therefore seemed worth while to direct attention to certain experimental results of a somewhat different kind which appear to show beyond cavil that modifications of characters sometimes result from crossing. The matter is an important one because it affects the old question of the swamping of new characters through crossing, as well as various other aspects of evolutionary theory.

¹ Read before the American Genetic Association, San Francisco meeting, August 3, 1915.

Anticipating the conclusions which will be reached in this paper, it may be pointed out that the swamping effect is not so serious a check upon progressive evolution as might be supposed, (1) because blending or modification of a new character only takes place in certain crosses and may be accompanied by segregation even in some of those, and (2) because Mendelian characters usually come out "pure" when crossed with the form from which they were derived. Hence when Mendelian characters arise through mutations in nature it may be expected that they will be able to perpetuate themselves and spread, especially when dominant, unless they place the organism at a disadvantage in the struggle for existence. The modification of a Mendelian character will come, not from crossing with its parent form but with a more distantly related species.

Some writers appear to believe that it is practically impossible to modify a unit character because it is represented in the germ plasm by a "gene" whose essential characteristic is its unmodifiability. But if we consider that each unit character is a *difference* which has arisen through a change in one element of the germ plasm, probably in a chromosome, then it would seem possible that if introduced into a foreign cytoplasm the chromosome may become subject to permanent modification.

Castle and Phillips (1914) have produced evidence from hooded rats tending to show that selection may modify a unit character in certain cases, although the nature of this result is not yet fully analyzed. They moreover show that the hooded character is modified by a cross. Davenport (1906) in his experiments with poultry, concluded that unit characters are frequently modified by crossing. He says (p. 80):

Very frequently, if not always, the character that has been once crossed has been affected by its opposite with which it was mated and whose place it has taken in the hybrid. It may be extracted therefrom to use in a new combination, but it will be found to be altered. This we

have seen to be true for almost every characteristic sufficiently studied—for the comb form, the nostril form, cerebral hernia, crest, muff, tail length, vulture hock, foot feathering, foot color, earlobe and both general and special plumage color. Everywhere unit characters are changed by hybridizing.

In crosses between *Oenothera rubricalyx* and *O. grandiflora* I have studied with care the modifications which take place in the expression of the various character-differences in F_1 , F_2 and later generations. Many of the results have been recorded in detail elsewhere (Gates, 1914, 1915a, pp. 250–282). It need only be said that the foliage characters in F_2 form an absolutely continuous series so that it is impossible to apply to them usefully the unit-character conception. In F_3 a large number of races were obtained differing in many ways as regards their foliage, many of them breeding true and others varying within wide or narrow limits. Occasionally in back-crosses an apparently complete reversion takes place to one or other of the parents, but blending and fractionation of the characters is the rule.

It is, however, difficult to obtain critical evidence from the foliage because, while the original differences are sharply marked, yet it is always possible to assume that the continuous F_2 series and the numerous F_3 races result from the presence of many independent units.² I will therefore confine my attention to the sharp pigmentation character (R) of *rubricalyx*, for in the inheritance of this character crucial evidence may be obtained. The origin of this dominant unit-character through a single mutation, and the subsequent attainment of the duplicate condition (RR') for this character in some of the offspring of later generations (1915b), have been pointed out elsewhere. Here we will examine the modifications of R which take place when *rubricalyx* is crossed with *O. grandiflora*.

The main facts regarding the variability of R in these

² The inheritance of pubescence-differences shows similar features and can not be reasonably interpreted in terms of numerous units.

crosses have already been published (Gates, 1914, p. 244 and 1915a, p. 257) and need only be summarized here, to emphasize their significance. In the publications cited I had not yet recognized that the occurrence of 15:1 ratios in later generations of *rubricalyx* is significant as indicating that in such families the duplicate condition for R had been reached, even although other ratios such as 5:1 occur as well.

The F₂ generation of the crosses between *rubricalyx* and *grandiflora* contained 2,794 plants, in 20 of which the red bud-character R showed decided modification so as to be more or less intermediate between the two parents. Since each plant in bloom produces scores of buds simultaneously, and hundreds during the season, there is ample material for determining the exact degree of modification or development of the character in every individual. As will be seen from the original records, the 20 plants in which the color pattern was more or less modified were not all alike but formed a series, some being nearer the normal R than others. In most other F₂ plants sharp segregation took place, the buds being entirely either R or r without the slightest doubt in classification. In addition to the 20 plants above mentioned, there were, however, a certain number in which the character R was more or less underdeveloped, so that it was impossible to be certain whether they represented mere fluctuations or real modifications of the character.

The crucial test of modification is supplied by the F₃ generation. Two of these last-mentioned intermediate plants self-pollinated yielded offspring like themselves, without any tendency to segregate into the R and r types. These families numbered, respectively, 283 and 20 plants, so that in the former case at least any tendency to segregation could not fail to be observed. The buds of these plants were intermediate, the pigmentation was pale and was never fully developed on the hypanthium as is the case in *rubricalyx*. The whole population was then intermediate like the parent.

Another F_3 family (No. 149) was derived from an F_2 plant (65. III. 12) having sepals weak red with the color pattern as extensive as in *rubrinervis* 6 (*i. e.*, nearly the extreme condition), and in addition streaks of pale red on the hypanthium. This plant was therefore nearer r than R , and one may account for its occurrence through "contamination" before segregation took place in the germ cells of the previous generation. In pure *rubrinervis* or *grandiflora* I have never found even a trace of red on the hypanthium until the flower fades. The offspring of this plant numbered 186 individuals and their pigmentation fluctuated about that of the parent plant as a mean. This condition closely approximated that in *Æ. rubrinervoides* (1915c, p. 390), which may have originated in a similar way.

We must, therefore, conclude that plants which are intermediate in pigmentation breed true, at least in all cases tested, and that the degree of pigmentation in the parent is adhered to in the offspring whether the parent plant is an under-pigmented R or an over-pigmented r . In this aspect, the inheritance in such cases is quantitative and the offspring vary only within narrow limits.

The quantitative aspect is further emphasized when F_1 and F_2 hybrids of *Æ. grandiflora* and *Æ. rubricalyx* are crossed back with either parent. The pigmentation is much intensified when crossed back with *rubricalyx*, and greatly diluted when crossed with *grandiflora*. Thus in $(rubricalyx \times grandiflora) \times grandiflora$ if the female parent is heterozygous for R , segregation into R and r plants will occur in the offspring, but the R plants will be much paler than in the selfed offspring of the female parent.

Hence there are two somewhat antagonistic effects which have to be considered, (1) the segregation of R and r individuals, and (2) a permanent dilution of the pigmentation of the R individuals. The former effect can be explained by the meiotic mechanism which segregates

chromosome pairs. The latter effect may be due to a modification of the chromosomes themselves, or perhaps of the surrounding cytoplasm, or the inhibition in pigmentation may be explained by the presence of more numerous *grandiflora* chromosomes. Everywhere, in an accurate study of the inheritance of R, the quantitative as well as the qualitative (presence or absence) aspect has to be considered.

The dilution effect from crossing back with *grandiflora* has been tested in six families numbering 673 individuals and is always essentially the same. Although segregation into the R and r types takes place when the parent is heterozygous, yet R once diluted always remains so and apparently never gives rise to the original deeply pigmented condition. In other words, a permanently blended condition arises as regards the depth of pigmentation, although this will still segregate from the unpigmented condition in heterozygous plants.

It is not easy to furnish a complete explanation for this diluting effect. The permanent dilution of R through union with a *grandiflora* germ cell may perhaps be accounted for by the fact that in the heterozygote the chromosomes of *grandiflora* are closely associated in the same nucleus with those of the other parent. The chromosomes which are finally dissociated in the germ cells, after thousands or millions of mitotic divisions in association, might then be supposed to be somewhat modified. There are, however, difficulties with this view, since the absence-character, r, is usually not contaminated, but splits out sharply and almost invariably without any trace of red-production.

It is also difficult to account for the facts on the assumption that the cytoplasm has been permanently modified.

There is, however, one hypothesis which appears to meet the case. If all the *grandiflora* chromosomes are equally effective in inhibiting anthocyanin production in

the hybrids with *rubricalyx*—a not improbable hypothesis—then the dilution effect will be the same in F_1 or in crossing back, whenever an R chromosome is present in the next generation; and when such a chromosome is not present there will of course be complete absence from the buds of the *rubricalyx* pigment. On this hypothesis, in an original cross between *rubricalyx* and *grandiflora* a certain (observed) reduction in pigmentation occurs. When the F_1 hybrid is crossed back with *grandiflora* the additional *grandiflora* chromosomes thus introduced dilute or inhibit the color still further, while the presence or absence of the diluted R will depend upon whether or not the R chromosome from *rubricalyx* is present. It would thus appear to be unnecessary to assume that this chromosome is itself modified by its different nuclear and cytoplasmic environment.

In other words, the *grandiflora* chromosomes may be supposed to exert a mass effect in inhibiting the influence of the R chromosome. It is, of course, possible that in these circumstances the R chromosome itself may be permanently modified, but it seems possible to explain all the facts without making this assumption. In any case, whatever the *modus operandi*, there can be no question that the R character is permanently diluted by crossing with *grandiflora*, and the degree of dilution is increased every time the hybrid is again crossed back with that species.

Another noteworthy fact is that as the pigmentation becomes more dilute its morphological expression is more irregular. The color pattern of the bud begins to break up, and instead of continuous pigmentation of the whole bud a patchy effect will be produced. This spotted condition of the buds is very marked in certain families, *e. g.*, in the second generation of offspring from (*rubricalyx* $\times$ *grandiflora*) $\times$ *grandiflora* (see Gates, 1915a, Fig. 113, p. 280). When it appears it is found to persist in later generations. To account for this condition through the

accession of a "spotting factor" is a gratuitous assumption. Spotting appears rather to be the manner of expression of the character when the amount of pigment is small. It must be said, however, that in some families having no greater quantity of pigmentation there is a strong tendency for it to remain uniformly distributed, so that the whole bud is very pale red.

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